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ACANTHODES LUNDI, NEW SPECIES (ACANTHODII), AND ASSOCIATED COPROLITES FROM UPPERMOST MISSISSIPPIAN HEATH FORMATION OF CENTRAL MONTANA

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Abstract

Acanthodes lundi is the first species of the genus recognized from the Mississippian of North America. It is characterized by a mosaic of angular, tightly bound tesserae on the head; position of the autopalatine ossification, which does not reach over the posterior end of the mentomandibular; expansion of the mentomandibular into a knob housing a large symphysial pit; weakly developed articular knob of the ceratohyal; tooth-like gill rakers with well-ornamented blades and unexpanded or only slightly expanded bases; hyomandibular rakers which are longer than those on the ceratohyal; and by the squamation development and the ossification of the endoskeleton, which were more rapid than in other *Acanthodes* species with known ontogenies. The morphology of the autopalatine ossification rules out the possibility of a palatoquadrate commissure having been present. The mentomandibular knob with a large symphysial pit indicates the existence of a basimandibular element. Associated coprolites are described as true excreta and one type of them is tentatively assigned to *A. lundi*. It is suggested that *A. lundi* was primarily macrophagous.

Introduction

Specimens of *Acanthodes* were collected in 1971–1978 by Richard Lund, Adelphi University, and John R. Horner, Princeton University, from the Heath paper shale of the Heath Formation, and by William G. Melton, University of Montana, from the Bear Gulch Limestone Member of the Heath Formation, at localities between Heath and

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Beckett, Fergus County, central Montana. The stratigraphy of the collecting area was discussed in connection with the description of faunal elements, sedimentology, and depositional history of the Bear Gulch Limestone by Melton (1969, 1971), Melton and Scott (1973), Scott (1973), Schram and Horner (1978), Williams (1979), and Horner (1980), and of the Heath shales (Heath Shale in previous terminology) by Schram and Schram (1974), and Horner (1980). Melton and Scott (1973) regarded the Heath Shale as Upper Mississippian, and the Bear Gulch Limestone as Lower Pennsylvanian in age, but Scott (1973) and Horner (1980) date both as uppermost Mississippian. According to Williams (1979) and Horner (1980), the Heath Formation is the uppermost unit of the Big Snowy Group and is unconformably overlain by the Pennsylvanian Tyler Formation of the Amsden Group. The Heath Formation can be divided into (ascending) Beckett, Bear Gulch, and Surenough members, which form lenticular bodies of carbonate sediments within the black shales of the formation. The fossil content indicates marine origin for all the shales except the *Acanthodes*-bearing paper shale, which is a freshwater deposit situated westward of, and correlative with, the Beckett lentil. The term ''Heath shale *Acanthodes*,'' used throughout this paper for brevity, is invariably meant to refer to the specimens of *Acanthodes* from the freshwater paper shale on the stratigraphic level of the Beckett Member.

The Bear Gulch Limestone specimens of *Acanthodes* are deposited in the Carnegie Museum of Natural History and at the University of Montana. Although acanthodian remains apparently are not uncommon in the Bear Gulch, their preservation is exceedingly fragmentary. I have examined the best preserved Bear Gulch specimens, UM 2958, UM 5535, and CM 30667. Of these UM 5535 is the most complete, but even it consists of only disrupted flank squamation, fragmentary tail, displaced pectoral spine, and an incomplete anal spine. It has an estimated total length of about 400 mm. Though UM 5535, as well as other Bear Gulch specimens in CM and UM collections, can be safely assigned to *Acanthodes,* they are specifically indeterminate. All hitherto known autochthonous occurrences of *Acanthodes* come from freshwater depositional environments, lacustrine, fluvial, and fluvial-deltaic (top-set depositional area) in character. Since the environment of deposition of the Bear Gulch was near-shore marine (Schram and Horner, 1978; Williams, 1979; Horner, 1980), it may be assumed that the specimens of *Acanthodes* were transported into it from streams postmortem, and their fragmentary preservation thus is not at all surprising. Because no aspect of morphology is either worth mentioning or can be satisfactorily described, the Bear Gulch specimens are not given further consideration in this paper.

According to W. D. Matthew's principle (Simpson, *in* Matthew and

Paula Couto, 1959:51; see also Baird, 1964:3), ''in a collection of uni-fied origin . . . congeneric animals will generally be of a single species, or, if they are of more than one species, the discontinuity between the groups will be large and evident. In such a collection, then, in the absence of fairly obvious discontinuity, the variation within a genus should usually be taken as intraspecific.'' The Heath shale *Acanthodes* specimens conform to Matthew's principle and for this reason they are assigned to a single species, *A. lundi,* described here for the first time. It is the first *Acanthodes* species recognized from deposits of Missis-sippian age in North America. The Heath shale collection contains a number of coprolites which are also described.

The *Acanthodes*-bearing paper shale is a dark green to black, very thinly laminated petroliferous shale, and the specimens are softer than the matrix. Many specimens are contained within the individual shale laminae and therefore can be seen only as silhouettes under the matrix; these have been prepared using Electro-Stylus and X-ACTO knives. The shale is quite soft, and it thus proved possible to expose some morphological features and dimensions that would be difficult to as-certain from X-ray prints.

SYSTEMATIC PALEONTOLOGY

Class Acanthodii
Order Acanthodiformes
Family Acanthodidae
Genus **Acanthodes** Agassiz, 1833
(Type species *A. bronni* Agassiz, 1833:20)

Note.—Most of our knowledge of *Acanthodes* is based on speci-mens from Lebach near Saarbrücken, West Germany, and, therefore, they are referred to in the account below. However, from Watson's (1937) description it is evident that the Lebach material comprises specimens with such wide proportional variations, unaccountable for by growth, that undoubtedly not one (*A. bronni*) but several species are present (Watson, 1937:95, Fig. 20, Pl. 14; see also Dunkle and Mamay, 1956; Zidek, 1975*b*, 1976). Because Agassiz's (1833–1844) syn-

types of *A. bronni* cannot be identified in the Lebach material, and because his description and illustrations are too inadequate to determine on which of the variations recorded by Watson the species had been based, it is impossible to erect a neotype, and, accordingly, *A. bronni* should be regarded as *nomen dubium.* For this reason the name *bronni* is used in quotes throughout this text.
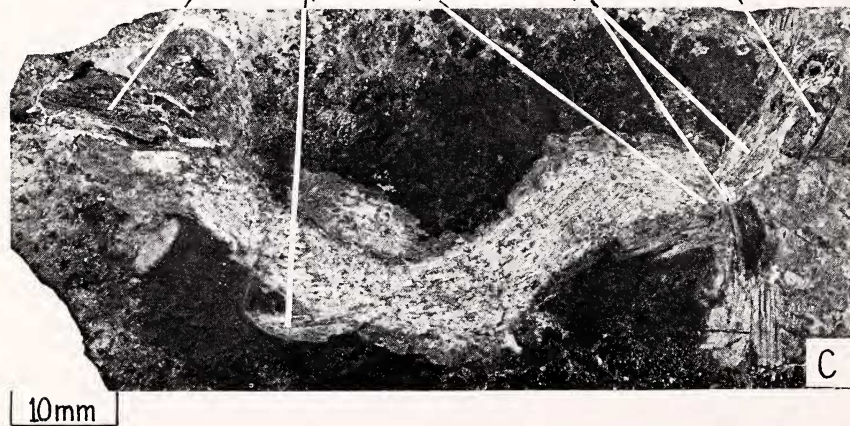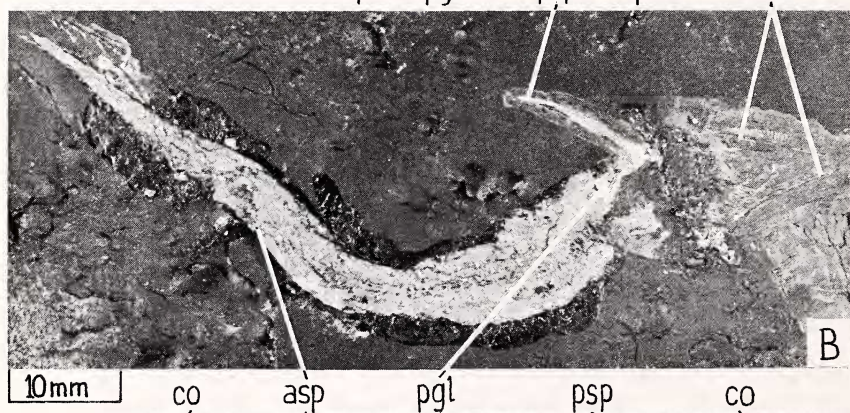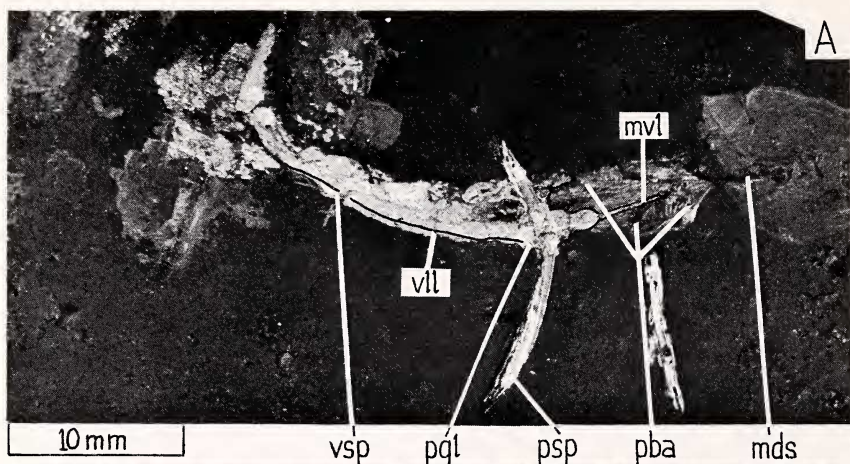
Acanthodes lundi, new species
(Figs. 1–6)

Holotype.—CM 25593, 215 mm in nose-to-caudal cleft length. This is the largest articulated specimen that, although incomplete in some respects, best represents the species.

Paratypes.—CM 25591, CM 25592, CM 25594 through 25596, CM 25598 through 25600, CM 25602, CM 25603A through H, PU 22296, PU 22297.

The CM 25603 suite comprises 73 specimens. Much of this suite consists of only patches of scales, detached and often fragmentary spines, and fragments of the endoskeleton which are too small to reveal anything concerning the morphology. Therefore, only the few 25603 specimens worth closer study were labeled individually, in alphabetical order.

Etymology.—Named in honor of Dr. Richard Lund, who has collected a majority of the specimens.

Horizon and Locality.—Heath paper shale (Beckett Member equivalent), Heath Formation, uppermost Mississippian, sec. 28, T. 14 N., R. 20 W., Fergus County, central Montana.

Diagnosis.—Head with a mosaic of angular, tightly bound tesserae; autopalatine does not reach over the hind end of the mentomandibular; mentomandibular anteriorly expanded into a knob housing a large symphysial pit; ceratohyal articular knob not pronounced; gill rakers toothlike, with ornamented blades and unexpanded or only slightly expanded bases; hyomandibular rakers one-fourth to one-third longer than those on the ceratohyal; squamation development and ossification of the endoskeleton more rapid than in *A. "bronni"* and *A. bridgei* (unknown in other *Acanthodes* species).

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Fig. 1.—*Acanthodes lundi,* new species. A, CM 25599 (estimated total length about 80 mm), anterior extent of squamation, median ventral sensory line, and ventrolateral sensory line are outlined; B, CM 25600 (total length 87 mm); C, CM 25598 (estimated total length about 100 mm). Abbreviations: asp, anal spine; co, coprolite; mds, mandibular splint; mvl, median ventral sensory line; pba, posthyoiden branchial arches; pgl, pectoral girdle; psp, pectoral spine; vll, ventrolateral sensory line; vsp, pelvic spine.
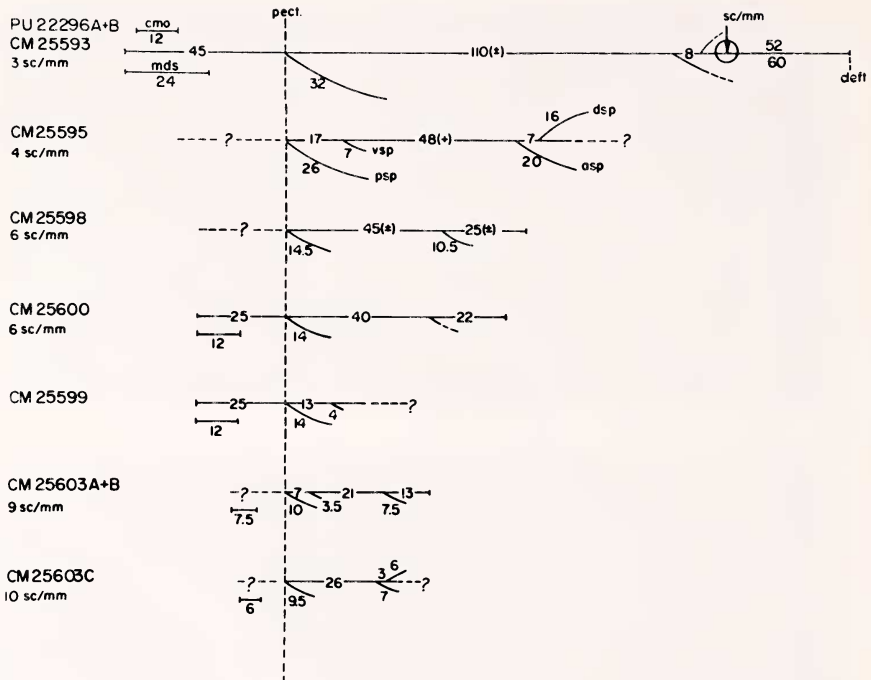
Fig. 2.—Schematic presentation of body proportions (measurements in mm) in *Acanthodes lundi,* new species. Scales per millimeter in a row (sc/mm) measured in the region of the largest scales, around the main lateral sensory line between the dorsal spine and the tail. Abbreviations: asp, anal spine; cmo, outer diameter of circumorbital ring; dsp, dorsal spine; mds, mandibular splint; psp, pectoral spine; vsp, pelvic spine.

DESCRIPTION AND DISCUSSION

Although even the best Heath shale specimens are incomplete in some respects (see Figs. 1, 5), they nevertheless provide the criteria necessary for species distinction. Among the features well enough preserved to warrant a description are the overall body proportions, the dermal bones of the head, certain parts of the visceral skeleton, the pectoral girdle, all the spines, and the squamation. The caudal fin (preserved in PU 22296 only) is too damaged to be described in any detail. Consequently, it is only noted here that a slight posteroventral expansion appears to have been present in the longitudinal division of the hypochordal lobe.

Size, Proportions, and Squamation

Of the available specimens only those listed in Fig. 2, ranging from 55 to 215 mm in nose-to-caudal cleft length, provide information on

the body proportions. These specimens do not represent the entire size range of the species, however. The largest detached pectoral spine in the collection (CM 25603H) is 55 mm long, indicating a fish over 300 mm long, and the largest detached scapulocoracoid (CM 25603G, Fig. 6A) is 16.7 mm in height, indicating a fish nearly 400 mm long. It can thus be concluded that *A. lundi* attained a size comparable to that of the other *Acanthodes* species (see Zidek, 1976, for review).

Despite the fragmentary preservation of all the specimens measured, the relative positions and sizes of the fin spines can be discerned. The single dorsal and anal spines are situated far posteriorly close to the tail; the anal spine is 15 to 20% longer and positioned somewhat more anteriorly than the dorsal. The pectoral spines are the largest and amount to 16% of the total specimen length, whereas the pelvic spines are the smallest and amount to only 27 to 35% of the length of the pectorals. The length of the anal amounts to 72 to 77%, and of the dorsal to 62 to 63%, of the length of the pectorals. The length ratios of the spines relative to each other, as well as the ratio of the pectoral spine length to the total specimen length, show no allometry for the sample.

The mandibular splint shows negative allometric growth of 3% in relation to the total specimen length. The maximum length of the branchiostegal rays amounts to 25% of the length of the mandibular splint regardless of the total specimen size (CM 25599, Fig. 1A; CM 25594, Fig. 5B), thus indicating zero allometry between the two. Prepectoral length can be measured in only three specimens, PU 22296, CM 25593, and CM 25600, in which it comprises 22, 22, and 29% of the total specimen length, respectively. The outer diameter of the circumorbital ring is available in only one articulated specimen, CM 25593, in which it amounts to 27% of the prepectoral length. The height of the scapulocoracoid amounts to 25 to 26% of the pectoral spine length in all the specimens studied, and it can thus be concluded that no allometry occurred in the size range represented. However, a negative allometry is indicated for the suprascapula in relation to the scapulocoracoid, as is evidenced by changes in morphology of the termination of the scapular blade during growth (see the section on pectoral girdle). The caudal fin is preserved only in PU 22296 (215 mm in total length), in which the distance from the cleft to the tip of the axial lobe is 25 mm, that is, approximately 12% of the total specimen length.

The only other acanthodian that has been adequately treated biometrically is *Acanthodes bridgei* from the Upper Pennsylvanian of Kansas (Zidek, 1976:24–27). *A. lundi* appears to differ from *A. bridgei* in having slightly shorter pelvic spines and in the dorsal spine being shorter than the anal. Apart from that, however, the two species are remarkably similar in their proportions. Although no measurements

are available for other *Acanthodes* species, it has long been thought that they all are proportionally close. The similarity in proportions of *A. lundi* and *A. bridgei* supports the notion of proportional uniformity of the genus.

The squamation consists of nonimbricating, minute scales with transversely rhombic, flat-to-convex, unornamented crowns. The morphology of the scales, as well as their size relative to the total specimen size, in no way differ from those previously described for *Acanthodes* (see Zidek, 1976:27–33), and, therefore, require no further comment. However, the rate of development of the squamation is of interest, for it was apparently so rapid in *A. lundi* that even the smallest specimen (CM 25603C, approximately 55 mm in total length) has its flank fully scaled. This specimen lacks most of the prepectoral region, nevertheless it is evident that the squamation reached the level of the pectoral girdle and began spreading anterior to it. The squamation is nearly fully developed in specimens only about 80 mm long (see CM 25599, Fig. 1A).

The scale counts per millimeter in a row (measured in the region of the largest scales, around the main lateral sensory line between the dorsal spine and the tail) conform closely with those previously reported for other North American *Acanthodes* species (Zidek, 1975*b*; 1976: Fig. 13). This demonstrates that in *Acanthodes* the scales increased in size by the addition of areal zones of growth to the crown throughout ontogeny, and that within certain ranges the scale counts can be used to estimate total specimen size but are of no value for species identifications.

Head and Visceral Skeleton

The preserved parts of the cranial and visceral skeleton include portions of the lateral-line sensory system, the circumorbital bones, a mosaic of minute tesserae, the jaws, the hyoid arch including the branchiostegal rays and the gill rakers, and a few posthyoidean branchial elements.

The suborbital and postorbital branches of the infraorbital line and the profundus line are the only parts of the lateral-line sensory system of the head preserved (Fig. 3A). The course of these canals and the morphology of the semicylindrical ossicles enveloping them differ in no way from the pattern previously described for *Acanthodes* (Zidek, 1976:9–13, Figs. 4C, 5, and references therein). The median ventral sensory line is well apparent in the branchial region of CM 25599 (Fig. 1A). Anterior to the pectoral girdle this line becomes surrounded by a bulge of scales and branches into the paired ventrolateral line as in other *Acanthodes* species (Miles, 1966:153; Zidek, 1976: Fig. 4C).
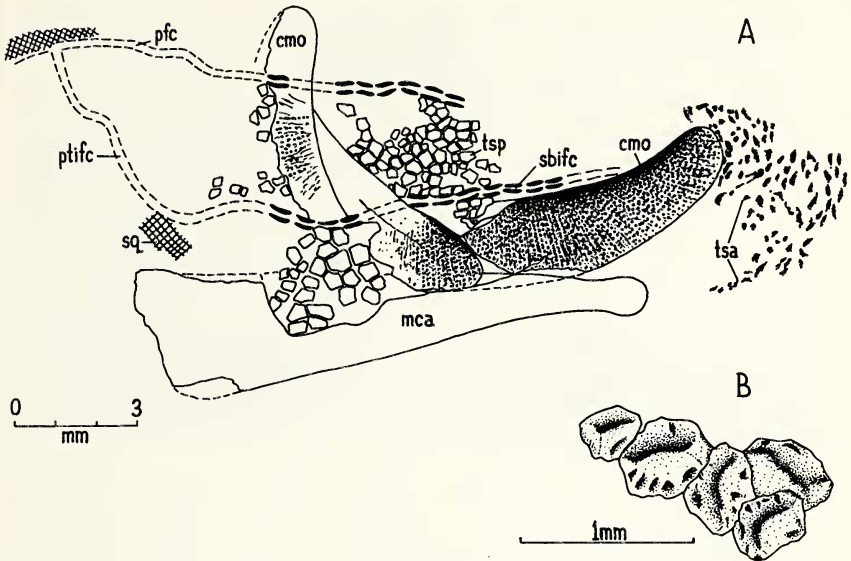
Fig. 3.—*Acanthodes lundi,* new species. A, head of CM 25593 (holotype) and B, detail of anterior tesserae in CM 25594. Abbreviations: cmo, circumorbital bones; mca, anterior meckelian ossification; pfc, profundus sensory line; ptifc, postorbital branch of infraorbital sensory line; sbifc, suborbital branch of infraorbital sensory line; sq, squamation; tsa, anterior tesserae; tsp, posterior tesserae.

The circumorbital ring is preserved, though incompletely, in only two specimens, CM 25593 (Fig. 3A) and CM 25594 (Fig. 5B). The individual bones are crescent-shaped, each with an elevated rim along the inner margin. Their entire surface is ornamented with radiating rows of minute tubercles which are most prominent on the inner rim. The projected meeting point of the radiating tubercle rows is well off the inner margin of each bone, toward the center of the orbit. Due to incomplete preservation it cannot be established whether the dimensions of the circumorbital bones were equal or unequal, and, consequently, whether there were four or five bones.

The tesserae are best seen in CM 25593 (Fig. 3A). This specimen affords some evidence that the squamation extended as far anteriorly as to the postorbital branch of the infraorbital sensory line and over the posterior part of the profundus canal. It is thus reasonable to conclude that the squamation passed into a shield of tesserae in the area between the postorbital canal and the orbit. As far as can be judged from CM 25593, the posterior half of the circumorbital ring was sur-
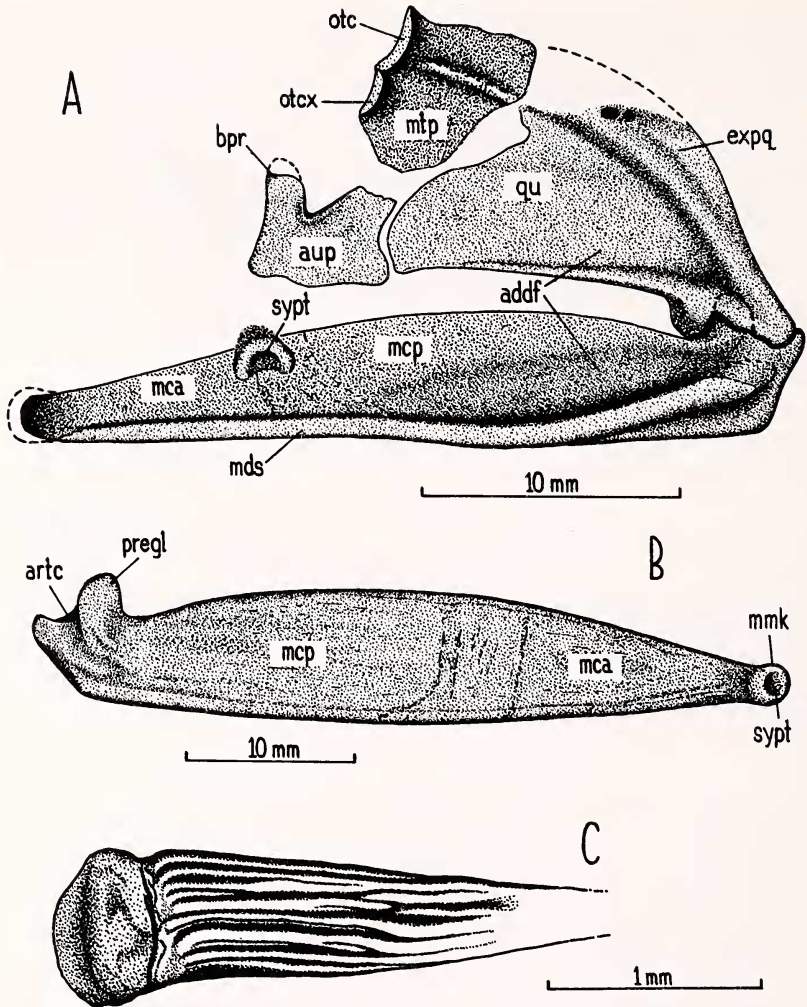
Fig. 4.—*Acanthodes lundi,* new species. A, restoration of upper and lower jaws in lateral view, based on CM 22596 (see also Fig. 5A) except for metapterygoid ossification from CM 25603D; B, CM 25603E, detached lower jaw in mesial view; C, hyoid gill raker from CM 25594. Abbreviations: addf, adductor fossa for m. adductor mandibulae; artc, articular cotylus; aup, autopalatine ossification of palatoquadrate; bpr, basal process; expq, extrapalatoquadrate crest; mca, anterior (mentomandibular) meckelian ossification; mcp, posterior (articular) meckelian ossification; mds, mandibular splint; mmk, mentomandibular knob; mtp, metapterygoid ossification of palatoquadrate; otc, otic cotylus; otcx, auxiliary otic cotylus; pregl, preglenoid process; qu, quadrate ossification of palatoquadrate; sypt, symphysial pit.

rounded by exceedingly thin, unornamented polygonal tesserae, whereas around the anterior margin of the ring and in the nasal region there was a cover of ornamented, roughly polygonal tesserae. Both the ornamented and unornamented tesserae range from 0.25 to 0.50 mm in diameter. The unornamented tesserae resemble those previously described for *Acanthodes* (Reis, 1896: Fig. 2; Watson, 1937:107–108; Zidek, 1975b: Fig. 2E; 1976: Fig. 5), however, they are not translucent at the margins, lack central depressions or any other irregularities in thickness, and are more distinctly angular forming a more tightly bound mosaic than in other *Acanthodes* species. In CM 25593 the anterior, ornamented tesserae are preserved only as irregularly shaped impressions. However, a small patch of anterior tesserae in CM 25594 (Fig. 3B) indicates that they are roughly polygonal in outline, with prominent, slightly arcuate crests and several minor depressions near the margins. Though there is no evidence of a grading together of the two types of tesserae, it appears likely that the entire head was covered with a dermal skeleton of tessellate pattern.

The jaws are preserved articulated in CM 25596 (Fig. 5A) and lack only the metapterygoid ossification. Fortunately, this ossification is exposed in lateral view in CM 25603D, whose quadrate is of the same size as that in CM 25596, thus allowing a composite reconstruction of the entire jaw apparatus (Fig. 4A). The jaws differ somewhat proportionally from those in *A. "bronni"* (Miles, 1968: Fig. 4A; 1973b: Fig. 12A, B) in that the entire anterior meckelian ossification lies anterior to the autopalatine ossification of the palatoquadrate. The lower jaw was, therefore, longer and the mouth was either only slightly subterminal or terminal in *A. lundi*. Though the CM 25596 jaws are only about half the size of those illustrated for *A. "bronni"* by Miles (1973b: Fig. 12A, B), the anterior and posterior portions of the lower jaw are perichondrally co-ossified and there is only a narrow gap between the quadrate and autopalatine ossifications of the upper jaw. As already shown, *A. lundi* attained a size comparable to that of *A. "bronni"*; it is, therefore, clear that in *A. lundi* the co-ossification started earlier in ontogeny and/or was more rapid than in later occurring species such as *A. "bronni"* or *A. bridgei*.

The autopalatine ossification definitely lacks a palatine process and a depressed area and/or groove for attachment of an anterior labial cartilage claimed for *A. "bronni"* by Jarvik (1977:205, Fig. 6B). The metapterygoid ossification has a well formed otic cotylus and a somewhat smaller auxiliary otic cotylus, and a groove for the efferent pseudobranchial artery (Jarvik, 1977, Fig. 6A). Despite the good preservation of this ossification, I have been unable to find the foramen for the *ramus mandibularis trigemini* that Miles (1964: Fig. 1; 1968:111, Fig. 1; 1973b: Fig. 12A) identified in *A. "bronni"*; there is, however,

a foramen located on the extrapalatoquadrate crest of the quadrate ossification.

The lower jaw (Figs. 4A, B, 5A, B) has a nearly flat lower margin and a distinctly convex upper margin (in lateral view); a mesiad curved anterior portion terminates in an expanded knob bearing a large symphysial pit. The meckelian cartilage is perichondrally ossified in two sections, a shorter anterior mentomandibular ossification and a posterior articular ossification. Except in CM 25603F, a detached lower jaw only 23 to 25 mm long, the two sections are perichondrally co-ossified; nevertheless, their boundaries are still discernible, as an intermediate zone of weakness is more readily subject to fragmentation. The mandibular splint (Figs. 4A, 5A, B) is a slender, entirely unornamented dermal bone only slightly shorter than the meckelian cartilage, with a minor sinusoidal curvature and a broader posterior end. The anterior three-fourths of the splint are attached to the ventrolateral margin of the meckelian cartilage, whereas the posterior fourth bends upward, is superimposed on the laterally expanded posterior end of the meckelian ossification behind the adductor fossa, and reaches close below the articular cotylus. The only specimen in which the mandibular splint remains attached to the meckelian cartilage is CM 25596 (Figs. 4A, 5A). In this instance the anterior end of the splint is broken off, but from its impression on the surface of the meckelian cartilage it is evident that its termination followed the mesiad curvature of the meckelian termination.

There is little difference in the lower jaw length to height ratios between A. "bronni," A. sulcatus, and A. lundi, however, the jaw of the latter maintains a higher profile through most of its length, giving it a more robust appearance. The longitudinally convex profile of the upper margin of the lower jaw and the relative size of the jaw joint correspond more closely to those in A. sulcatus (Miles, 1966: Fig. 5) than to those in A. "bronni" or A. bridgei, in which the preglenoid process appears to have been larger and the anterior termination somewhat upturned (Miles, 1973b: Fig. 12; Zidek, 1976: Fig. 3).

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Fig. 5.—Acanthodes lundi, new species. A, CM 25596, and B, CM 25594, exposed in lateral view. Abbreviations: aup, autopalatine ossification of palatoquadrate; br, fragments of epi- or ceratobranchials; cbr, first ceratobranchial; cha, anterior ceratohyal ossifications; chp, posterior ceratohyal ossification; cmo, circumorbital bones; ebr, epibranchials; hgr, hyoidean gill rakers; hmv, ventral hyomandibular ossification; mc, meckelian cartilage; mca, anterior meckelian ossification; mcp, posterior meckelian ossification; mds, mandibular splints; mtp, metapterygoid ossification of palatoquadrate; pgl, pectoral girdle; psp, pectoral spine; qu, quadrate ossification of palatoquadrate; rbr, branchiostegal rays; rd, radialia.

A

10mm   aup br mc qu mds mtp ebr? psp cmo pgl rd psp

B

10mm   hmv chp mcp hgr rbr cbr cha mca
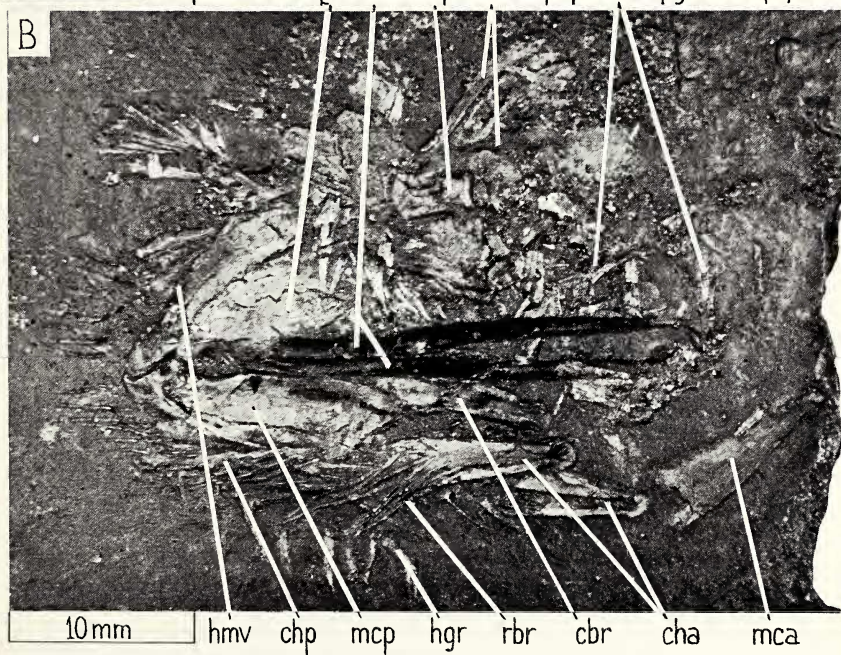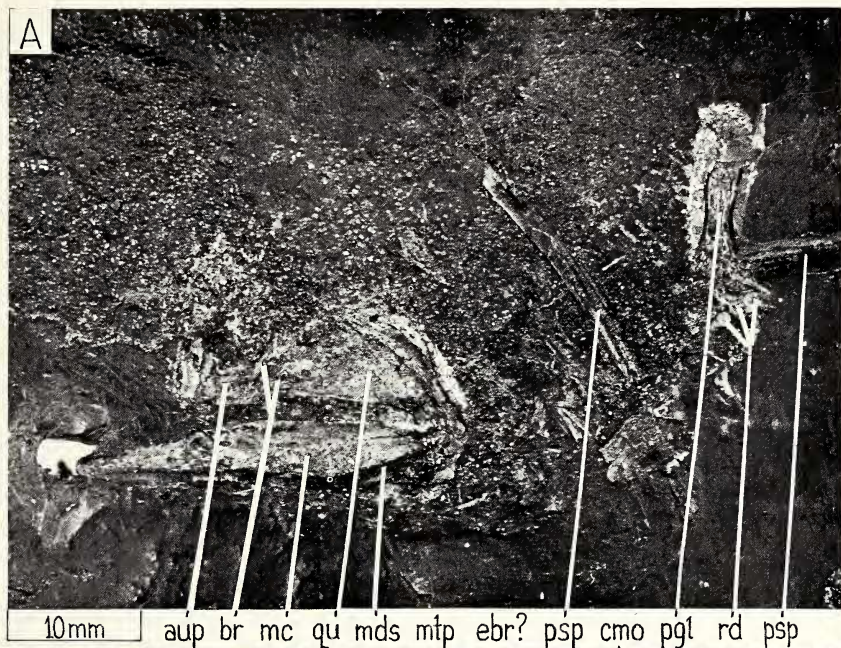
The feature by which the *A. lundi* lower jaw differs most markedly from other *Acanthodes* species is the presence of a mentomandibular anterior knob which bears a large symphysial pit (Fig. 4B). Watson (1937:103) noted that in the Lebach *Acanthodes* the lower jaw "becomes extremely slender anteriorly, where it is slightly turned inward and bears a very small pit, presumably for the short ligament by which it was attached to its fellow of the opposite side." A similar small pit is indicated, though not labeled, in figures of *A. "bronni"* by Reis (1891: Fig. 8d; 1896: Pl. 6, Fig. 1). In contrast to specimens of *A. "bronni"* described by Reis and Watson, the anterior meckelian termination in *A. lundi* does not narrow but expands and the symphysial pit is large. The anterior meckelian termination is, as a whole, reminiscent of the anterior ceratohyal knob for articulation with the basihyal in *A. "bronni"* (Miles, 1968: Fig. 2) and the symphysial pit in the lower jaw of certain crossopterygians such as the porolepiform *Holoptychius* (Jarvik, 1963: Fig. 15B; 1972: Fig. 47A, B; Jessen, 1966: Fig. 14B; 1967: Pl. 3B; Lehman, 1966: Fig. 58B), and, to a lesser degree, the coelacanth *Nesides* (Jessen, 1966: Text-fig. 15J, Pl. 22, Fig. 3).

According to Miles (1968:112), there is no definite evidence of the basimandibular element identified by Dean (1907:212, Fig. 12) in *A. "bronni"*. Dean's figure shows this element as a small ossification corresponding in size to the mentomeckelian of, for example, *Amia* (Goodrich, 1958: Fig. 430; Devillers, 1958: Fig. 408), but this interpretation is clearly a misconception resulting from a fracture in his specimen. Despite the absence of a basimandibular in *A. "bronni"* and, as far as we know, in all other Pennsylvanian and Lower Permian *Acanthodes* species, the presence in *A. lundi* of the mentomandibular (mentomeckelian) anterior knob with a large pit in its anteromesial face is strongly indicative of such an element. The mentomandibular knob and pit are so strikingly similar to the ceratohyal knob and fossa for articulation with the basihyal in *A. "bronni"* that the assumption of them serving only a ligamentous connection between the mandibular rami seems highly unlikely.

The hyoid arch can be seen in CM 25594 (Fig. 5B). This specimen shows the anterior ceratohyal ossifications of both sides (=hypohyals of Watson, 1937, and Nelson, 1968, 1969), traces of the right posterior ceratohyal ossification, and a small part of the right ventral hyomandibular ossification. The length of the ceratohyal amounts to approximately 80% of the lower jaw length (as in *A. "bronni,"* see Miles, 1973*b*: Fig. 15). The anterior ceratohyal ossifications gradually taper anteriorly, curve mesiad, and their mesial faces bear grooves "for, *inter alia,* the insertion of the anterior interhyoideus musculature" (Miles, 1968:113). In contrast to *A. "bronni,"* in which the anterior ends of the ceratohyals are expanded into large articulation knobs

(Miles, 1968: Fig. 2), in *A. lundi* the ends are unexpanded, round, and bear flat, anteromesiad oriented facets for articulation with the basi-hyal. Judging from the size of the associated pectoral spine (36 mm long), CM 25594 was 220 to 230 mm in total length. Because the anterior and posterior parts of the ceratohyals are not co-ossified in this specimen, it is clear that co-ossification (Miles, 1968:113, 1973*b*: 93) occurred late in ontogeny, only in the largest individuals. The only visible part of the hyomandibula is the lower end of its ventral ossification, yet it is situated substantially above the jaw joint. Even when the ceratohyal is restored to its proper position (Miles, 1973*b*: Fig. 15), there still remains a large gap between its posterior end and the lower end of the ventral hyomandibular ossification. The mutual position of the two elements thus invites the assumption that an accessory element was present between them, such as an interhyal (=stylohyal or symplectic, see Miles, 1965:241; 1973*b*:93).

The branchial region is partially preserved in CM 25599 (Fig. 1A) and to a very small extent in CM 25594 and CM 25596 (Fig. 5A, B). CM 25599 is far too small (80 mm in total length) to have any of the branchial arches ossified; it shows only a mass of gill rakers which are not distinct enough to allow determination of their orientation or morphology. CM 25594 shows the right anterior ossification of the first ceratobranchial and incomplete, displaced elements which most likely are epibranchials; CM 25596 contains only fragments of epi- or ceratobranchials. The anterior ossification of the first ceratobranchial (=hypobranchial of Watson, 1937, and Nelson, 1968, 1969) is very similar in size, mesiad curvature, and morphology of the anterior end to the ceratohyal, but lacks the gradual tapering characteristic of the ceratohyal. Instead, the tapering is confined to the posterior third of its length and the remainder is uniform in thickness. The true first hypobranchial, restored but at the same time doubted by Miles (1973*b*:97, Fig. 18) for *A. "bronni,"* is definitely not present in *A. lundi.*

The skeletal support of the integumental gill cover consists of a series of slender, well spaced branchiostegal rays carried by the hyoid arch (CM 25599, Fig. 1A; CM 25594, Fig. 5B). Regardless of the size of the specimen, the rays reach a maximum length of one fourth that of the mandibular splint. The lower, ceratohyal part of the series contains twenty gently sinusoidally curved, virgaform rays, whereas in the upper hyomandibular part there are only seven shorter and angularly bent virgaform-to-acinaciform rays (see McAllister, 1968, Fig. 1 for terminology). Thus, the branchiostegal rays of *A. lundi* are indistinguishable in shape and relative size from those in the specimens of *Acanthodes* from the Upper Pennsylvanian of New Mexico (Zidek, 1975*b*:12, Pl. 1E; 1976:13, Fig. 4A).

Of the gill rakers, only those of the hyoid arch of CM 25599 (Fig. 1A) and CM 25594 (Figs. 4C, 5B) are well enough preserved to allow description. They have the appearance of slender, laterally compressed, tapering tooth-cusps; they are about five times longer than wide, have short, unexpanded or only slightly expanded bases, and the entire blade is ornamented by longitudinal ridges (Fig. 4C). The grooves separating the ridges are as wide as the ridges. Though some of the ridges anastomose, most remain well defined throughout the length of the blade. In contrast to other *Acanthodes* species in which the rakers on the hyomandibula are shorter than those on the cerato-hyal (Watson, 1937:105; Miles, 1968:113; Zidek, 1976:14), the hyo-mandibular rakers are about 30% longer than those of the ceratohyal. Further, the rakers differ from those of other *Acanthodes* species in the prominence of the base and in the height to width ratio, outline, and ornamentation of the blade. The height to width ratio and the ornamentation of the rakers are the same in *A. "bronni"* and *A. lundi,* but in *A. "bronni"* the blades are leaf-like and basally constricted (see Reis, 1896: Pl. 6, Figs. 3, 18; Watson, 1937:105; Miles, 1968:113). In *A. bridgei,* on the other hand, the height to width ratio is much greater (12:1), the ornamentation consists of sparse and interrupted striae only, the blade is saber-shaped, and the base is much more prominent (Zidek, 1976:14, Fig. 4B). Our present knowledge of the morphology of the gill rakers is unfortunately limited to only a few *Acanthodes* species, nevertheless the above comparisons indicate its potential usefulness in diagnosing species.

The hyoidean gill rakers were inserted on the inner side of the arch and projected anteroventromesiad on the hyomandibular and antero-dorsomesiad on the ceratohyal (Fig. 5B; for *A. "bronni"* see Watson, 1937:105, Text-fig. 18; Nelson, 1968:140; Miles, 1968:125; 1973b:94). It is clear, therefore, that contrary to the recent claim by Jarvik (1977:210) the hyoidean gill rakers belong to the anterior series. I agree with Miles (1964, 1968, 1973b) that they projected into the pharynx and indicate the existence of a large hyoidean hemibranch.

The branchiostegal rays were first correctly identified as belonging to the hyoid arch by Reis (1891: Figs. 6a, 8d), who, however, changed his mind and identified them in all his later works as attached to the mandibular splint. Watson (1937:104, Text-figs. 18, 19) also erred in regarding the branchiostegals as inserting on the lower surface of the splint, and, consequently, believed that the gill cover was mandibular rather than hyoidean. Although the hyoidean nature of the acanthodian gill cover has more recently been confirmed by several lines of evidence (Stensiö, 1947; Denison, 1961; Jarvik, 1963; Miles, 1964 through 1973b), the attachment and orientation of the branchiostegals have never been precisely determined. In CM 25594 (Fig. 5B) the branchio-
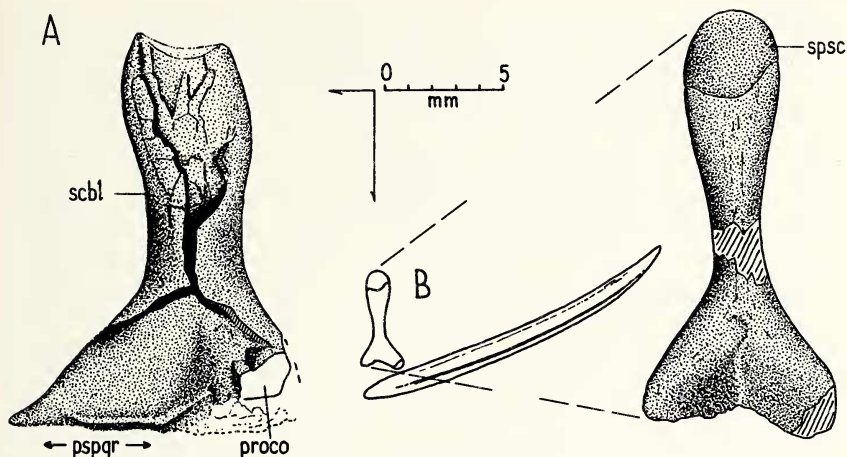
Fig. 6.—Pectoral girdle of *Acanthodes lundi,* new species. A, CM 25603G, anterolateral view of detached right scapulocoracoid of a size indicating a fish nearly 400 mm long; B, CM 25600, left girdle and pectoral spine from a juvenile 87 mm long (see Fig. 1B). Abbreviations: proco, procoracoid process; pspgr, pectoral spine groove; scbl, scapular blade; spsc, suprascapula.

stegals are attached to the outer side of the ceratohyal in a line that changes from ventrolateral on the anterior ossification to dorsolateral on the posterior ossification; the anterior rays exhibit mesiad curvature. On the ventral hyomandibular ossification the insertions cannot be seen, but presumably they were situated laterally or posterolaterally. The branchiostegals of the anterior ceratohyal ossification thus pointed ventromesiad, and posteriorly their orientation gradually changed to posteroventromedial and posteroventral on the posterior ceratohyal ossification, and eventually to posterior on the hyomandibula.

Pectoral Girdle

The pectoral girdle is preserved in CM 25591, 25593, 25596, 25598, 25599, and 25600 (Figs. 1A–C, 5A, 6B), and in several other instances as an isolated element. The isolated scapulocoracoid CM 25603G (Fig. 6A) is 16.7 mm in height and indicates a fish nearly 400 mm long, whereas in CM 25599 (Fig. 1A), which is about 80 mm in estimated total length, the size of the scapulocoracoid plate indicates that the entire girdle was probably no higher than 2.5 mm. The pectoral fin is partially preserved in only two instances, as a short, proximal series of fin rays in CM 25593 and as radials in CM 25596 (Fig. 5A).

Though the pectoral spine has not been found in place, in several

specimens it is preserved in close proximity to the girdle and both elements are sufficiently complete to consider their size relationship. The height of the scapulocoracoid amounts to 25 to 26% of the pectoral spine length in all the specimens studied, and no differential growth occurred in the size range represented (see Fig. 2). However, some differential growth undoubtedly occurred between the scapulocoracoid and the suprascapula. The suprascapula is not co-ossified with the scapular blade and is missing in all but one specimen (CM 25600, Fig. 6B). Nevertheless, the differential growth can be demonstrated by comparing the upper parts of the scapular blades of small and large specimens. Whereas in small, juvenile specimens the dorsal termination is the point of maximum diameter of the blade (Fig. 6B), in large specimens the level of maximum diameter is the subterminal, barrel-shaped portion of the blade (Fig. 6A). Consequently, the large girdles could not have accommodated suprascapulae as large relative to the scapulocoracoids as the small girdles, indicating negative allometric growth of the suprascapula. The shift in level of the maximum diameter of the scapular blade during ontogeny also accounts for the slender versus robust appearance of the blades in small and large girdles, respectively, although their height to maximum diameter ratio does not change appreciably during growth.

The dorsal margin of the scapular blade is higher posteriorly. The blade is circular in cross section and gradually narrows ventrad before expanding again into the scapulocoracoid plate. The surface for articulation of the fin skeleton (*margo radialis*), the ventral (coracoid) part of the plate, and the procoracoid are not represented in any of the specimens at hand. The remaining, discernible features of the scapulocoracoid plate are the procoracoid process and the upper margin of a groove that housed the pectoral spine (Fig. 6A). The mesially located subscapular fossa that leads to the coracoid foramen in the ventral muscle fossa (see Miles, 1973a:153, Text-fig. 19) is seen only in CM 25599. The procoracoid process is seemingly larger than in other *Acanthodes* species, but this is not certain since the articular surface may have been enlarged by postmortem abrasion.

On two previous occasions I noted a process-like extension posterolateral to the procoracoid process and interpreted it tentatively as either a laterally extended surface of the scapulocoracoid plate capping the pectoral spine or as an accessory dorsal articulation surface for the procoracoid (Zidek, 1975a:143, Fig. 5; 1976:16, Fig. 7C). No such extension is present in the *A. lundi* girdles, in which the upper margin of the pectoral spine groove is a rim that at no point becomes prominent laterally.

In summary, the pectoral girdle of *A. lundi* does not deviate in any available aspect of its morphology from that of most *Acanthodes*, in

which the suprascapula does not co-ossify with the scapular blade. Except, perhaps, for the lack of the lateral extension of the scapulo-coracoid plate there is nothing in the morphology of the girdle to serve distinction on the species level.

Concluding Remarks

Apart from the recorded North American occurrences of *Acanthodes* (Zidek, 1975*a*, 1975*b*, 1976, and references therein; Dalquest and Emsoff, 1977), detached spines assignable to this genus have been found also in deposits of Pennsylvanian (Westphalian D) age at Dominion, Nova Scotia (D. Baird, personal communication), and at several locations and stratigraphic levels in the Ohio Pennsylvanian (OU Ay-9 and OU Cc-4 from the Dorr Run and Washingtonville Shales in the Allegheny Series, and OU Aa-38 and OU Ale-19 from the Portersville and Brush Creek Shales in the Conemaugh Series). Because the pectoral girdle recently described from the Lower Mississippian (Tournaisian) of Nova Scotia (Zidek, 1977) cannot be identified any closer than as Acanthodidae, *Acanthodes lundi* remains the only species of the genus known from deposits of Mississippian age in North America. It should be emphasized, however, that in terms of the European standard stratigraphic section even this species is Upper Carboniferous, Namurian A or early B, in age.

The earliest unquestionable record of *Acanthodes* is *A. sulcatus* from the Lower Oil Shale Group of the Calciferous Sandstone Series, Viséan B, Mississippian, of Scotland (Miles, 1966:174; 1970:344; Paton, 1976:17). Unfortunately, this species is inadequately known and can be compared with *A. lundi* in only a general manner. The original diagnosis of *A. sulcatus* (Agassiz, 1835:125), based on only a patch of scales long since lost, was revised by White (1937:412), who selected a neotype and provided its measurements. From these measurements it appears that *A. sulcatus* is similar to *A. lundi* in overall body proportions, pectoral spine length to total length ratio (17%), pelvic spine to pectoral spine length ratio (29%), and prepectoral to total length ratio (only 41%). Both the anal and dorsal spines of *A. sulcatus* are thus approximately 20% shorter relative to pectoral spine length than in *A. lundi*. In addition, the two species differ in the position of the pelvic spines, and in the morphology of the pectoral girdle and jaws. The pelvic spines of *A. sulcatus* are situated well behind the pectoral spines, nearly half way between them and the anal spine (White, 1937:412, Text-fig. 1; Miles, 1970, Fig. 5), whereas in *A. lundi* the distance between the pectoral and pelvic spines is only about one fourth of the pectoral-anal distance (see Fig. 2). The scapular blade of *A. sulcatus* is slender, straight, and dorsally unexpanded. Its dorsal termination is rounded and apparently includes the suprascapular;

nothing is known of the scapulocoracoid plate. In contrast, the scapular blade of *A. lundi* is dorsally expanded and not co-ossified with the suprascapula. Judging from the illustration of *A. sulcatus* jaws by Miles (1966, Fig. 5), the metapterygoid ossification does not seem to have a well defined auxiliary otic cotylus and the mentomandibular ossification is anteriorly pointed instead of expanded as in *A. lundi*. According to White (1937:412), the scales of *A. sulcatus* ''occasionally show the faint median depression which Agassiz (1835, p. 125) so much emphasized in his original description, but this is certainly not peculiar to the species and may not be even characteristic.'' The posterior position of the pelvic spines and the near absence of the auxiliary otic cotylus are features atypical of *Acanthodes* and raise doubt as to the assignment of *A. sulcatus* to this genus. However, the final systematic placement of *A. sulcatus* will have to await a restudy of the type material.

The most obvious diagnostic feature of *A. lundi* is its lower jaw with the longitudinally convex profile of the upper margin and the anterior termination expanded into a knob housing a large symphysial pit. Other diagnostic but less obvious features include: the position of the autopalatine ossification, which does not reach over the posterior end of the anterior meckelian ossification; the tightly bound mosaic of tesserae, which are distinguishable from other species by their even thickness and angularity; the anterior end of the anterior ceratohyal, which is not expanded into a large articular knob; the tooth-like gill rakers with ornamented blades and unexpanded or only slightly expanded bases; the hyomandibular rakers, which are one-fourth to one-third longer than those on the ceratohyal; and the development of the squamation and the ossification of the endoskeleton, which are more rapid than in other *Acanthodes* species with known ontogenies. The mentomandibular knob with its large symphysial pit is a decidedly primitive feature that underwent reduction early in the history of the genus and whose resemblance to the ceratohyal-basihyal articulation (*A*. ''*bronni*'') adds weight to designating the meckelian element as a ceratomandibular. The tessellate pattern of the dermal skeleton of the head, the upper versus lower jaw proportions, and the rapidity of development of the squamation and ossification of the endoskeleton may also be regarded as primitive for the genus. Whether the morphology of the anterior termination of the ceratohyal (which may or may not be related to the morphology of the mentomandibular termination) and the relative size and morphology of the gill rakers are primitive features cannot be properly evaluated until more is known about the other *Acanthodes* species.

The length of the fin spines and the co-ossification of the mentomandibular and articular divisions of the lower jaw early in life cannot

be used taxonomically. In comparison to *A. bridgei* the pelvic spines of *A. lundi* are somewhat shorter relative to the pectoral spines and the dorsal spine is shorter than the anal, instead of being equal to it in length. However, for the pelvic spines the difference is not great enough to be considered diagnostic. Moreover, due to our lack of knowledge of intraspecific variability, the pectoral to pelvic spine length ratio is of dubious taxonomic value unless significantly different from anything so far known. The equal length of dorsal and anal spines in *A. bridgei* is an exception rather than the rule in *Acanthodes*. In most species the dorsal spine is shorter than the anal and *A. lundi* thus shares this character with the majority of *Acanthodes* species. The early co-ossification of the two divisions of the lower jaw in *A. lundi* may prove to be diagnostic, but this can only be determined after a more complete growth series becomes available. None of the measurable specimens so far available have the lower jaw preserved, and the isolated jaws allow for only rough estimates of the total specimen size.

Denison (1963:149) remarked that in the Acanthodii "no clear trends are indicated, though the best preserved and presumably the most strongly mineralized endoskeletons occur in the latest genus [*Acanthodes*]." Based on this statement, Moy-Thomas and Miles (1971:75) advanced the idea that the heavy ossification of the endoskeleton in *Acanthodes* compensated for the reduction of the exoskeleton. Ørvig (1951:415) concluded, however, that "the latter Acanthodians are presumably derived from forms which, besides a subperichondral calcified layer, also had a perichondral bone layer on their endoskeleton," and consequently that "the absence of perichondral bone must therefore in all probability be regarded as secondary." Studies of growth series of *A. "bronni"* (Watson, 1937), *A. bridgei* (Zidek, 1976), and *A. lundi* show that, although the ultimate extent of ossification of their endoskeleton was similar, they differ in the time ossification was initiated in ontogeny. This is particularly apparent with respect to the ossification—and perichondral co-ossification—of the neurocranium and jaws, which started later in life in the geologically younger species. In my opinion, these observations are best interpreted as a tendency toward retrogressive ossification of the endoskeleton. If true, current data for *Acanthodes* would appear to be in closer accord with those of Ørvig (1951:415; although perichondral bone is present in *Acanthodes*) than with those of Moy-Thomas and Miles (1971:75). This is not to say, however, that the inverse developmental relationship suggested for the two skeletal divisions by Moy-Thomas and Miles should be altogether rejected. Despite the apparent regressive trend in endoskeletal ossification, taken as a whole, *Acanthodes* may well have had a more strongly mineralized endoskeleton than other acanthodians. Unfortunately, our knowledge of the endoskeletons of the geo-

logically older acanthodians is too vague to recognize trends in their mineralization.

HEATH SHALE COPROLITES

The Carnegie Museum of Natural History collection of Heath shale *Acanthodes* contains numerous coprolites. In addition to twenty un-cataloged, isolated coprolites, a number of coprolites are associated with the CM 25603 suite of *Acanthodes* specimens, and a coprolite is present in the tail region of CM 25598 (Figs. 1C, 7D). All the coprolites are contained within the shale laminae and only their rough outlines are visible. Because manual removal of the firmly adhering shale matrix is exceedingly time consuming and difficult, this was done only for CM 25598, in which the presence of delicate skeletal remains did not allow alternate methods of preparation. The uncataloged, isolated coprolites were boiled in hydrogen peroxide and the remaining shale was removed ultrasonically. Specimens prepared in this way are whitish instead of their original dark brown color and reveal all the minute surface features (Fig. 7A–C).

Longitudinal, transverse, and diagonal sections of three uncataloged specimens revealed a total lack of internal structure. The structureless interior is in strong contrast to fine preservation of the minute external features. On these grounds the specimens may be designated as true coprolites (excreta) rather than enterospirae (fossilized intestines). A mass spectrographic analysis showed major amounts of phosphorus, silicon, iron, sodium, calcium, and aluminum, minor amounts of magnesium and manganese, and a trace of copper. These findings are essentially in accord with those of Williams (1972:16) and of the earlier writers cited by him. X-ray diffraction showed the presence of dahllite, a carbonated calcium phosphate.

The specimens range from 22 to 42 mm in length. Many have collapsed and the width thus can be determined in only a few. In those retaining a more or less round cross section the diameter is about one-fourth the length (Fig. 7A, D). In these relatively undistorted specimens the anterior end (the end pointing anteriorly while still inside the intestine) is more acutely pointed than the posterior end. Whorls are invariably present; they vary between two and six in number, are widely spaced, and extend through much of the specimen length. On the basis of these features, all the specimens examined may be regarded as spiral coprolites belonging in the amphipolar category of Neumayer (1904)—as opposed to his heteropolar category, which includes specimens with more numerous, closely spaced whorls concentrated on one end of the coprolite.

Subparallel folds diagonal to the long axis are readily apparent in a great majority of the specimens. They consist of broad ridges of low
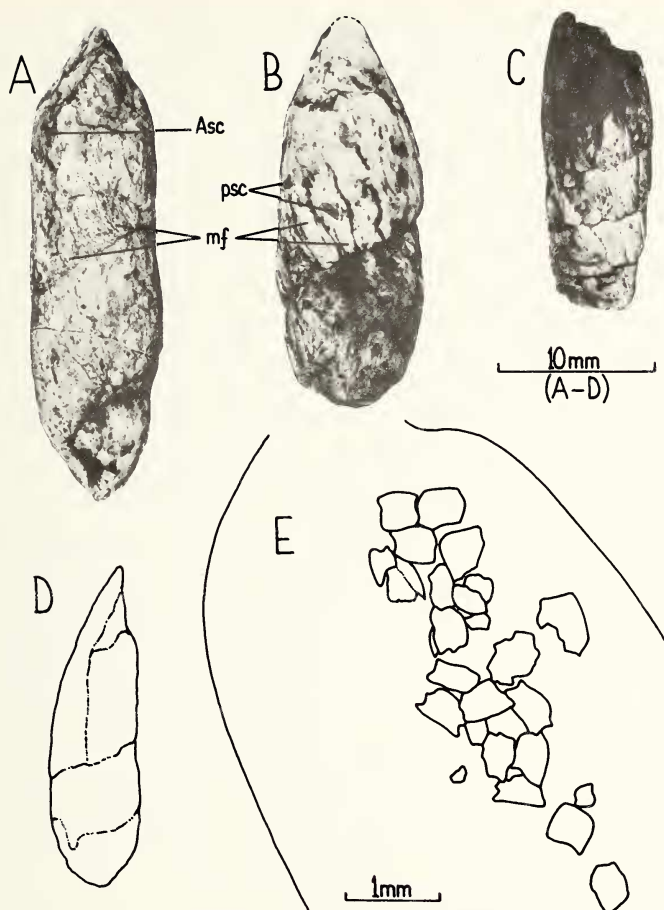
Fig. 7.—Representative specimens of Heath shale coprolites, all with anterior ends facing upward. A, D, and E are cylindrical specimens regarded as belonging to *Acanthodes lundi,* B and C are conical specimens which may be of palaeoniscoid derivation or a fish group hitherto unknown from the Heath shale. Note well developed secondary folds in A, and accumulation of *Acanthodes* scales in E. A, B, C, and E are uncataloged, isolated CM specimens and D is associated with CM 25598 (see Fig. 1C). Abbreviations: Asc, *Acanthodes* scales; mf, impressions of mucosal folds; psc, palaeoniscoid scales.

relief that are separated by narrow grooves and are continuous throughout the height of the whorls. The angle between the long axis and these folds cannot be measured accurately, for their course is oblique-to-meandering. Nevertheless, it can be said that the angle in no instance exceeds 45 degrees and in most instances is no more than

30 degrees. According to Williams (1972:13), such folds "are usually interpreted as sculpturing produced by the passage of fecal material over the mucosal folds but may also represent casts of mucosal folds on the outer sheath of the intestine." The mucosal folds of the spiral valve are continuous with those of the sheath, but the orientation of the two is not the same; the folds of the spiral valve run perpendicular to the passage of the fecal material, whereas those of the intestinal sheath are essentially parallel to that passage (Williams, 1972:12, Fig. 8A). From this it follows that no distinct markings could result from the passage of fecal material over the mucosal folds of the spiral valve. Because the movement would be taking place in a direction essentially perpendicular to the course of the mucosal folds of the valve, the only markings that could be present are those resulting from interruptions, if any, in the course of the folds. These would doubtless be minute, irregularly distributed, and most likely rare. Moreover, such markings would be discernible only in a still functioning intestine; postmortem, they would be quickly obliterated by the mucosal folds of the valve imprinted perpendicularly over them. It thus follows that the mucosal folds of the intestinal sheath should be considered responsible for the folds of the coprolites. Differentiating between sculpturing produced by the passage of fecal material over the mucosal folds and casts of mucosal folds is in essence a distinction between life and death, respectively. Williams' (1972) explanation of the external folds in enterospirae as casts of mucosal folds is therefore undoubtedly correct. In contrast to enterospirae, however, the Heath Shale specimens are true coprolites and the folds they exhibit could have been produced only by bowel action. They are best explained as sculpturing produced by the passage of fecal apatite paste over the terminal mucosal folds of the intestinal sheath. The low relief, or occasionally even partial obliteration, of the folds may be attributed to their compression during the passage through the anal sphincter muscle, as well as to the subsequent fossilization processes.

The morphology of the folds is not quite the same in all the specimens. In some they are clearly delineated and their surface is smooth (Fig. 7B, C), whereas in others they are barely distinguishable and their surface is wrinkled by minute, secondary folds (Fig. 7A). The secondary folds are especially prominent near the margins of the whorls and can be explained either by presence of secondary mucosal folds, or by a higher degree of compression causing the secondary wrinkling during the passage of fecal material through the sphincter muscle. Until the latter alternative is proved correct, the possibility of the secondary folds having taxonomic significance cannot be wholly discounted.

Because scattered palaeoniscoid scales are associated with Heath

shale *Acanthodes* specimens, consideration must be given to the possibility that some or all of the coprolites are of palaeoniscoid derivation. Williams (1972:9, 17) concluded that the palaeoniscoid valvular intestine probably was of the simple type seen in the modern gar. However, the hitherto known palaeoniscoid coprolites are heteropolar (Fritsch, 1895, Text-fig. 303, Pl. 123; 1907: Pl. 11, Figs. 1, 12; Heyler, 1969: Pl. 14, Fig. 1; Štamberg, 1976: Pl. 1), and their morphology is nearly identical with the Kansas Pennsylvanian enterospirae that Williams (1972) compared with the spiral valves of modern elasmobranchs and tentatively assigned to the xenacanth sharks. To my knowledge, none of the heteropolar coprolites associated with palaeoniscoid specimens have been sectioned, but their morphology and their position with respect to the body of the fish leave little doubt that they are fossilized intestines. It thus appears that in at least some palaeoniscoids the spiral valve was a structure as complex as that in elasmobranchs. Increased complexity of the valve results in increased resistance to the passage of its contents, which may be regarded as one of the reasons why "the material egested from the cloaca of a shark is either in liquid or loosely viscous form" (P. W. Gilbert, personal communication *in* Williams, 1972:9). If so, it then would be perfectly logical to conjecture that palaeoniscoids possessing more complex spiral valves did not produce solid excreta. On the other hand, the coprolite *Coprolithes rugatus,* described by Fritsch (1907:19, Pl. 11, Fig. 5) and tentatively assigned by him to *Acrolepis,* is very similar to the specimen shown here in Figure 7C.

The above discussion serves to illustrate the hazards of making taxonomic assignments for isolated enterospirae and, even more so, for true coprolites. First of all, there is no guarantee that the two categories of spiral coprolites recognized by Neumayer (1904), heteropolar and amphipolar, represent in all instances enterospirae and excreta, respectively, and this distinction should thus be viewed only as a generalization that may not always be valid. This problem has already been elucidated by Williams (1972:17), who emphasized the necessity of microscopic study of the internal structure in determining the true nature of coprolites. Secondly, the spiral valve is known to be extremely variable within a genus and even intraspecifically (Parker, 1885). Further, for physiological reasons it is to be expected that intestinal contents would at times vary in consistency, which in turn would result in varying morphologies of the excreta of an individual. Therefore, determination of the original bearer of a detached enterospira or the producer of an isolated coprolite can only be tentative, even when faunal analysis and skeletal inclusions of the coprolites are considered.

In the Heath shale coprolites the skeletal inclusions consist of small

palaeoniscoid and *Acanthodes* scales; no fragments of invertebrates have been found. The palaeoniscoid scales are distributed more or less evenly among the successive whorls (Fig. 7B, C), whereas the *Acanthodes* scales occur in small patches that are concentrated near the anterior end of the coprolites (Fig. 7A, E). The two types of scales have not been found occurring together. The presence of *Acanthodes* remains in the body cavity of a palaeoniscoid (Traquair, 1879) and, conversely, of palaeoniscoid remains in the body cavity of *Acanthodes sulcatus* (Watson, 1937:115; Miles, 1968:124; Moy-Thomas and Miles, 1971:76) indicates that the two types of fish had occasionally fed on each other. However, this by no means implies that the Heath shale coprolites containing palaeoniscoid scales are to be attributed to *Acanthodes* and vice versa. Cannibalism is widespread among modern fish, sometimes involving individuals of almost equal size, and there is no reason to assume that this was not the case among the Heath shale acanthodians or palaeoniscoids. It is thus clear that identification of skeletal inclusions alone cannot serve as a means for establishing the derivation of the coprolites. Further mention of the CM 25598 may be of some help here, because it is the only instance in which a coprolite is closely associated with skeletal remains of *A. lundi*. If the CM 25598 represents a fish in natural association with its excretum, then it would follow that egestion and death occurred almost simultaneously. Since the coprolite could not be sectioned, it cannot be said with absolute certainty that it is a true excretum, nor can it be conclusively shown that its association with the fish is natural. Nevertheless, there is some evidence favoring the true coprolite—natural association thesis: a) the position in the tail region of the fish (Fig. 1C) is atypical of enterospirae; b) other, sectioned specimens of the same external morphology are true excreta; and c) coprolites of the same external morphology as is that of CM 25598 are associated with many of the *Acanthodes* specimens in the CM 25603 suite, but never with the scattered patches of palaeoniscoid scales from the same locality.

The CM 25598 is about 100 mm in estimated nose-to-caudal cleft length, and the coprolite associated with it is 28 mm long and has a maximum diameter of 7 mm. The morphology of this coprolite (Fig. 7D) is very similar to the uncataloged, isolated specimens shown in Figures 7A and E which contain only *Acanthodes* scales; these, in turn, are distinguishable from those of Figures 7B and C which contain only palaeoniscoid scales. The specimen of Figure 7A is 32 mm long and 9 mm in maximum diameter and the largest scales it contains are 0.25 mm broad. The specimen partially shown in Figure 7E is 42 mm long and 10.5 mm in maximum diameter and the largest scales it contains are 0.5 mm broad. The scale sizes may be converted into scale counts of four scales per millimeter in a row for that figured in 7A and

two scales per millimeter in a row for that figured in 7E, which indicate fish about 140 and 250 mm long, respectively. Because the scales measured may not represent the largest body scales of the ingested fish, the total length estimates are to be regarded as minimal. It follows from this that the fish that produced the 33 mm long coprolite swallowed an *Acanthodes* at least 140 mm long, and the one that produced the 42 mm long coprolite swallowed an *Acanthodes* at least 250 mm long. There is no way to determine the size of the predators, except for concluding that they were larger than the prey. The predator-prey size difference may not have been substantial, however, because acanthodians and palaeoniscoids had large jaw gapes. Based on the above discussion, the coprolites of Figures 7A, D (CM 25598) and E are tentatively identified as produced by *Acanthodes lundi* preying on smaller individuals of its own species. They represent one of two morphological types of coprolites found in the Heath shale collection and can be characterized by a cylindrical shape with the anterior end more acutely pointed than the posterior end, two or three whorls only, and the possible presence of secondary folds. The second type of coprolite, which includes those of Figures 7B and C, is characterized by a conical shape, a higher number of whorls (up to six), and well defined, smooth folds (secondary folds are absent). This type may be of palaeoniscoid derivation, but the possibility cannot be discounted that it belongs to a group of fish hitherto unrecorded from the Heath shale. The presence of only *Acanthodes* scales in the cylindrical coprolites and only palaeoniscoid scales in the conical coprolites, as well as the absence of invertebrate inclusions, may be due to an insufficient number of specimens studied.

To my knowledge, the only acanthodian coprolites described to date are two specimens from the Upper Carboniferous of Bohemia, Czechoslovakia. Both are associated with, and undoubtedly derived from, *Acanthodes* and were named *Coprolithes acanthodi* by Fritsch (1907:20, Pl. 11, Fig. 8, Pl. 12, Fig. 17). As far as can be discerned from the poor figures given by Fritsch, the specimens are broken longitudinally and show short series of imbricating cones. It thus appears that they are enterospirae and, therefore, cannot be compared with the Heath shale specimens.

The genus *Acanthodes* is generally regarded as microphagous; the few fossils which document the ingestion of large prey by *Acanthodes* have been interpreted as indicating atypical behavior (Miles, 1968:124; Moy-Thomas and Miles, 1971:76). The thesis of typically microphagous habit has been accepted because of the edentulous condition of the genus, but this may not be entirely correct. Jaw teeth are not necessary for swallowing a large prey, and *Acanthodes* is known to possess well developed gill rakers which could have assisted in holding

the prey. The derivation of the Heath shale cylindrical coprolites implies that considerable differences in diet may have existed among *Acanthodes* species. The species possessing long, slender gill rakers may have been primarily microphagous, whereas those possessing shorter, tooth-like gill rakers may have been primarily macrophagous. *Acanthodes lundi* belongs in the latter category.

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